Updated SLR definition and additional metrics on herbivory

Jade, Jul 16

To make our metrics comparable to Neo's, from now on I will focus on subsets of the food web where all species are connected to at least one other species. In other words, plant species that are not eaten by any other species will be left out in calculating SLR. In addition, metrics on herbivory are calculated: 1) the fraction in number of plant species that are eaten by other species (herbivore or omnivores); 2) the fraction in plant biomass that is eaten by other species. The effect of the key parameters (D_r, γ and τ_u) on the metrics will be tested.

1 Result

The algorithm has been improved so that it takes 1/4 the time to simulate a community of the same size. A wider range for γ and D_r as well as a larger community size can thus be used (previously it takes > 3 hours to simulate a 30 species community with a $\gamma < 0.1$ and $D_r < 0.3$).

1.1 D_r and γ effect

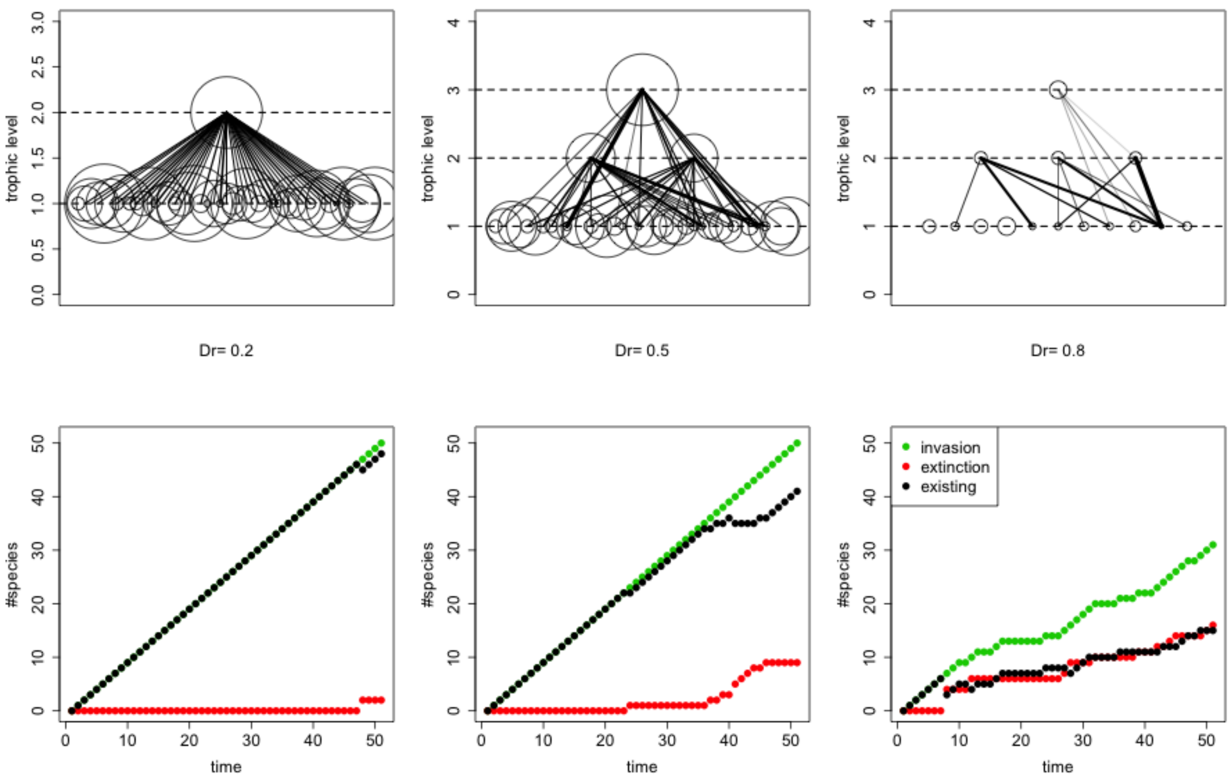

Fig. 1 The effect of D_r on the food web structure

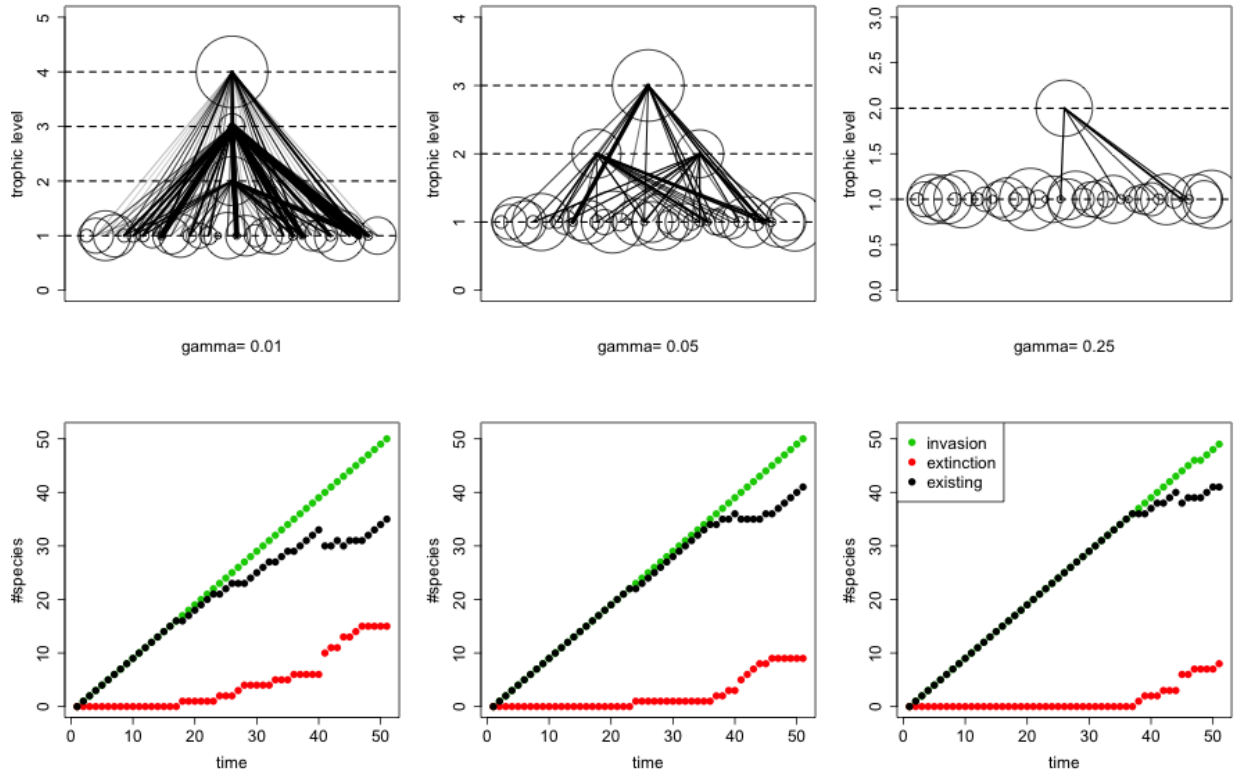

Fig. 2 The effect of D_r on the food web structure

With a wider range of γ for comparison we can see a pattern that was not clear before: the higher the γ, the higher the number of species eventually included in the community. Since a higher γ also leads to fewer trophic links, this result suggests a bigger contrast in the slope of the link-species relationship between different γs than previously inferred.

1.2 Link-Species Relationship

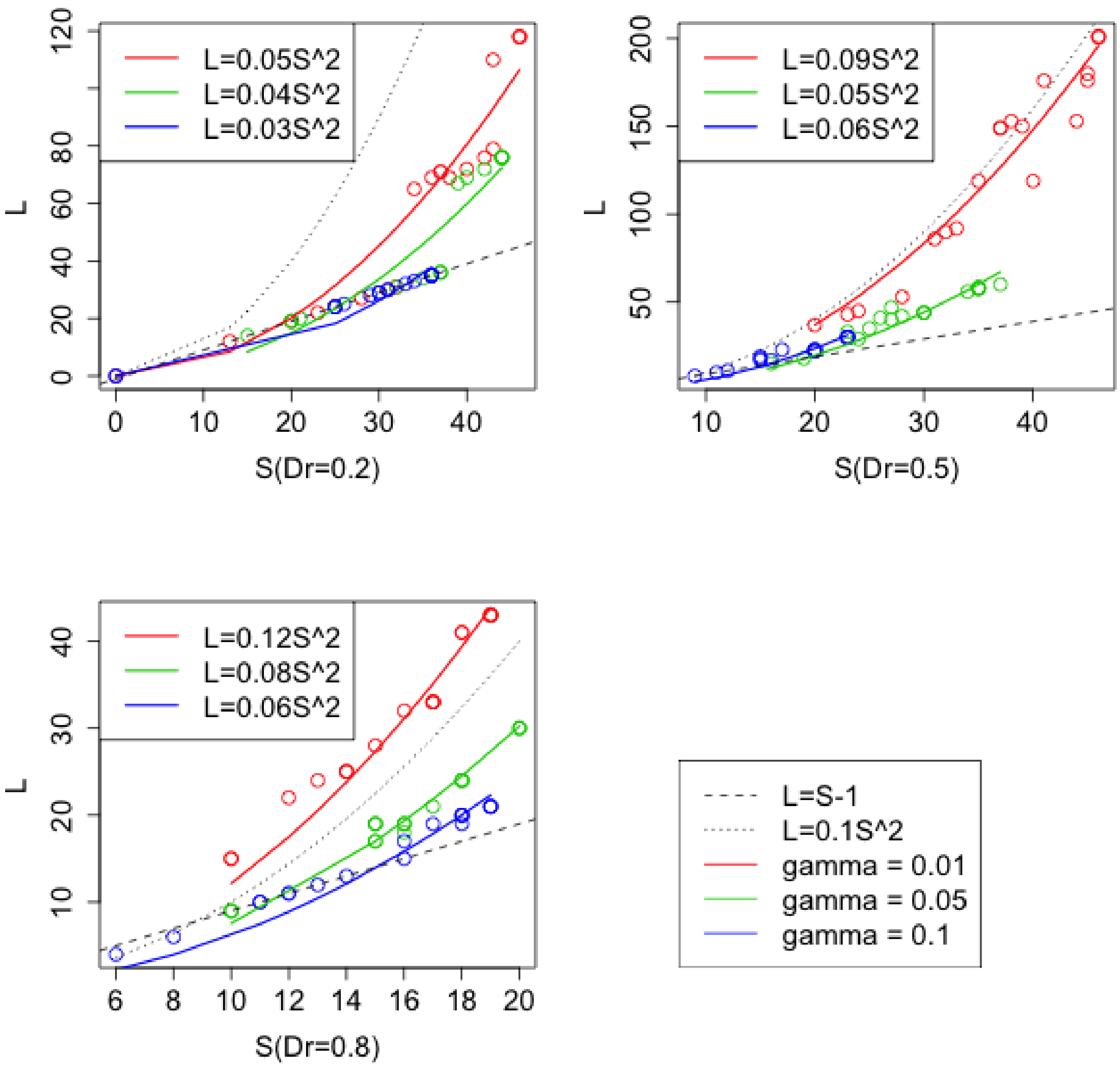

Fig. 3 Link-species relationship ($\tau_u = 0.1$)

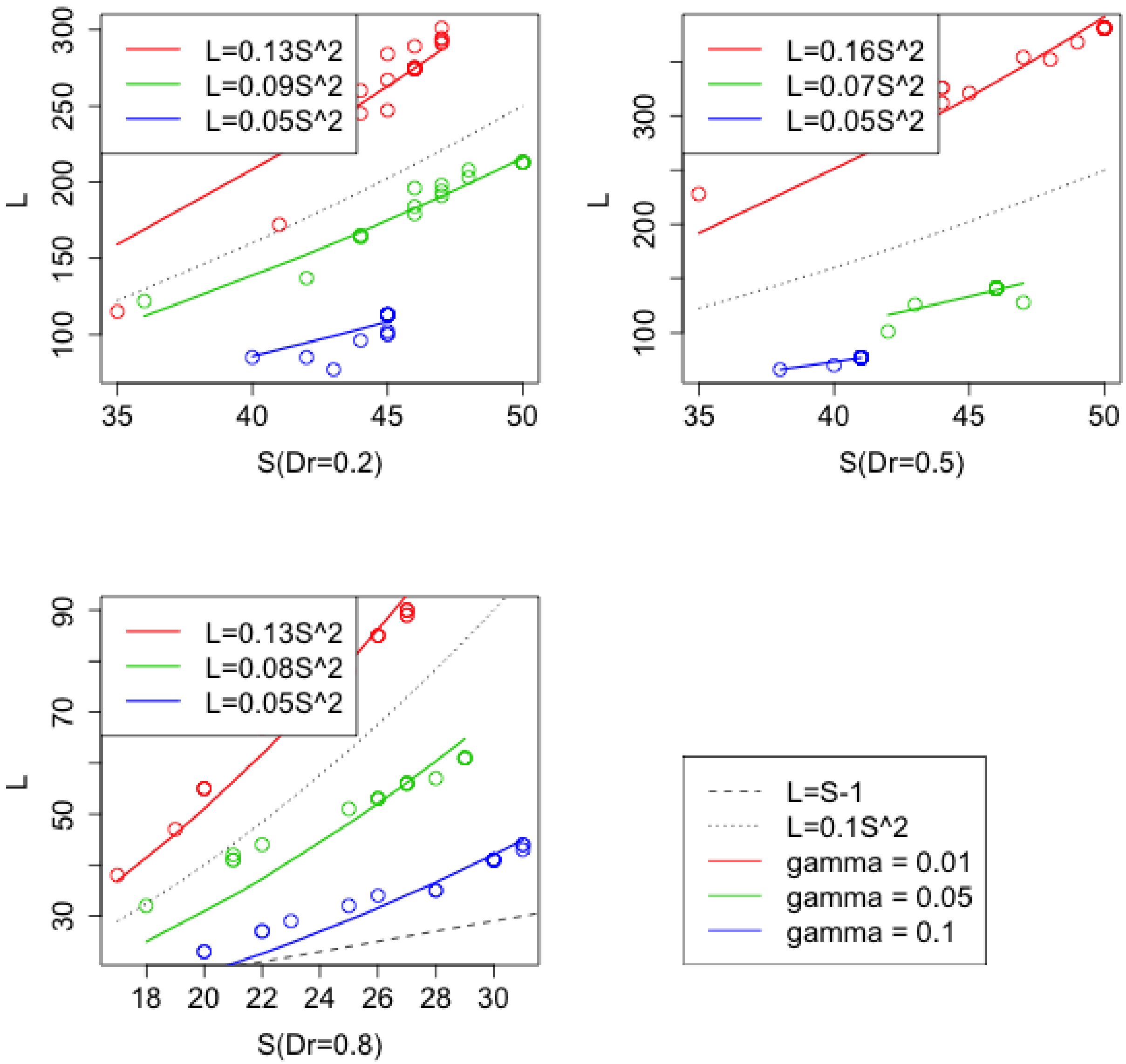

Fig. 4 Link-species relationship ($\tau_u = 0.15$)

With the updated definition of LSR (not counting plant species that are not eaten by any species), the slope is lower (compared to Scenario 1 in July 3 write-up) and in general more quadratic ($L = aS^2$) than linear. As before, the higher the τ_u, the steeper the LSR (bigger a). When $\tau_u = 0.1$, the effects of γ and D_r are similar as before: higher γ leads to slower (smaller a) while higher D_r leads to steeper LSR (bigger a). When $\tau_u = 0.15$, while the effect of γ is the same, the effect of D_r is not significant.

Notice that for $\tau_u = 0.1$ and $\gamma = 0.1$, some of the communities have dropped below the lower boundary, or $L < S - 1$. This is because for these communities, there are independent components that are not connected to each other. For example, if there is a herbivore not preyed by any predator and feeds on a plant species that is not consumed by any other herbivores, these two species form a component that is not connected to any other species in the food web. Allowing this kind of situation, the minimum number of links a food web with S species has is $L_{min} = S/2$, in which case the food web is separated into $S/2$ independent components each with two species connected to each other but not to any other species. But as we can see, that seldom happens.

1.3 Herbivory fractions

Here I have calculated two fractions about herbivory: first, the fraction in number of plant species that are preyed on by other species (herbivore or omnivores); second, the fraction in plant biomass that is eaten by other species. In the following I will address the former as F_1 while the latter as F_2.

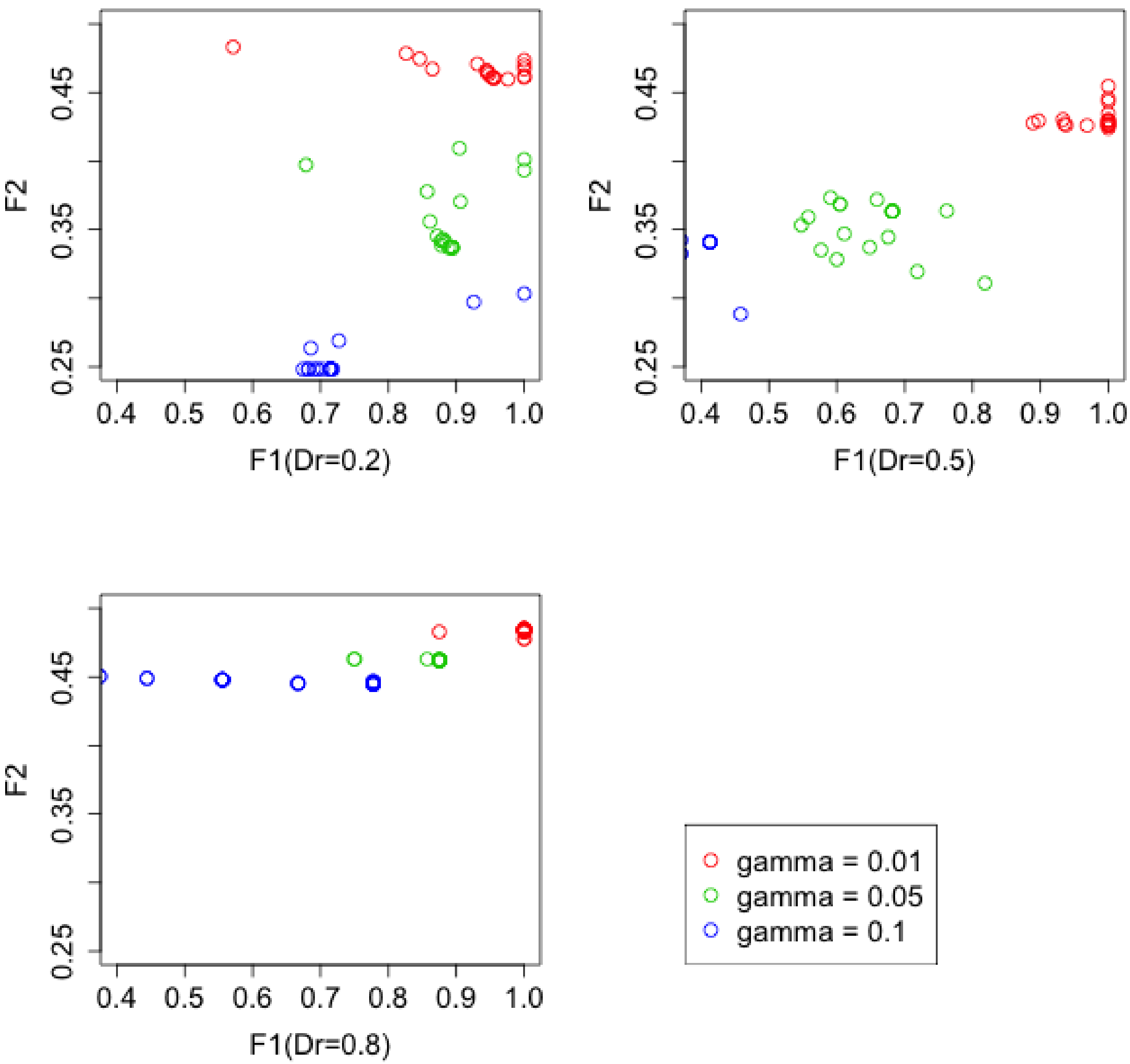

Fig. 5 Herbivory fraction mapping ($\tau_u = 0.1$)

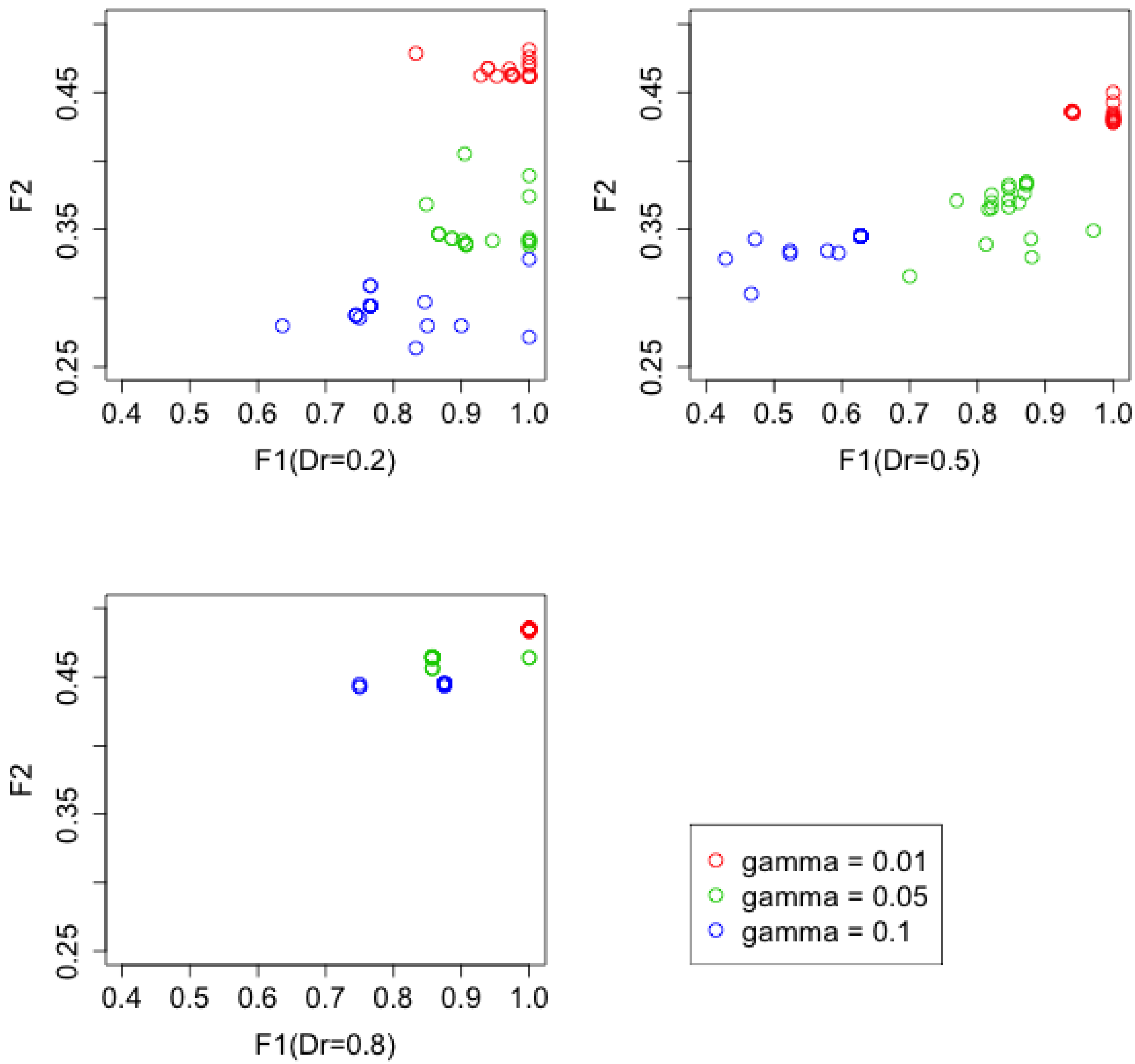

Fig. 6 Herbivory fraction mapping ($\tau_u = 0.15$)

From the graphs we can see that F_1 and F_2 are in generally positive correlation (although not significant when $D_r = 0.2$). The most striking pattern is that the bigger the γ, the lower the F_2, which is indicated by the clear vertical separation of dots in different colors (different γs). The effect of γ on F_1 is less significant: bigger γ leads to significantly lower F_1 only when D_r is 0.5 or 0.8 but not when $D_r = 0.2$. The effect of D_r is in general less straightforward: it depends on the value of γ and is not always linear, e.g. when $\gamma = 0.01$, the lowest F_2 appears for $D_r = 0.5$ instead of when D_r is the lowest ($= 0.2$) or the highest ($= 0.8$). One less ambiguous pattern is that F_1 and F_2 are both the highest when D_r is high.

With this result, the high F_2 (fraction being eaten in total plant biomass) in the tropics can be associated with a low γ or non-intermediate D_r (high or low). The issue is complicated by the in conceptual ambiguity of γ and D_r (please see discussion 2.2 below).

2 Discussion

2.1 Analytical approximation of the mean number of prey for each species

The analytical solution of MERA to the steady state abundance is:

$$SSN_i = \sum_{p}^{P_i} (C'_p \theta_{c,i})^{\frac{1}{D_{r,i}-1}} \tag{1}$$

where P_i is the total number of prey species for species i, $\theta_{c,i}$ is the capture-adjusted resource requirement, defined as

$$\theta_{c,i} = \frac{\theta_i}{\tau_{c,i}} = \theta_i e^{\gamma \sum_p^{P_i} D_{r,p}} \tag{2}$$

Assuming all species have the same θ and D_r (and therefore the i subscript will be suppressed), from Eqs. 1 and 2 we get:

$$SSN = P(C'\theta_i e^{\gamma P D_r})^{\frac{1}{D_r - 1}} \tag{3}$$

To maximize SSN, I equal the derivative of SSN over P to zero:

$$\frac{\partial SSN}{\partial P} = \frac{P\gamma D_r}{D_r - 1}(C'\theta_i e^{\gamma P D_r})^{\frac{1}{D_r - 1}} + (C'\theta_i e^{\gamma P D_r})^{\frac{1}{D_r - 1}} = 0 \tag{4}$$

From which we can solve for the P that maximizes SSN_i:

$$P_{optimal} = \frac{1 - D_r}{\gamma D_r} \tag{5}$$

We can see that, although derived from an approximation that all species have the same θ and D_r, Eq. 5 is consistent with the general patterns demonstrated in the simulation: the smaller the γ and D_r, the more preys a species tends to have and therefore better connected the food web is.

The more accurate measure of connectedness should be the average number of prey per species. From the result section 1.1 we can see that a higher γ leads to a higher total number of species. This means that the effect of γ on the overall connectedness (indicated by the number of prey per species) of the food web is unambiguously negative: a smaller γ will always result in a better connected food web because there are fewer species with a higher optimal number of prey; a bigger γ will result in a poorly connected food web because there are more species with a lower optimal number of prey.

In contrast, the effect of D_r on the overall connectedness of the food web is unclear. With D_r increasing, both the number of species and the optimal number of prey decreases, generating opposing effect on the number of prey per species. This might be the reason why the metrics respond to D_r in less straightforward and non-linear ways.

2.2 Are γ and D_r independent?

Here is a conceptual conundrum: if we accept the interpretation of D_r as the level of generalization (so that generalists have higher D_r than specialists), it seems that γ is not independent from D_r but rather correlated. To see this, recall that by definition, a higher γ means higher cost in extending food source to include one additional species. The question is, should this cost be higher, lower or the same for specialists compared to generalists?

Naturally we would think it's higher, since specialists are less diverse or flexible to prey on different species. If that is the case, why is it that not all species are generalists with higher D_r when it means all gains, i.e. higher competitiveness, less chance to be preyed on (since it causes higher cost in capture efficiency for the predator) and less cost in having more prey species (and therefore access to more resource) and no downsides at all? The upside of being a specialists with lower D_r has not been reflected in the current formula anywhere.

Whatever the answer might be, clarifying the interpretations and underlying connections between γ and D_r will enormously help reduce the uncertainty in model assumptions and facilitate future empirical tests.